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THE FAMILY LITTORINIDAE IN THE INDO-PACIFIC

Part II. The Subfamilies Tectariinae and Echininae

by JOSEPH ROSEWATER

Division of Mollusks
National Museum of Natural History
Washington, D.C. 20560 U.S.A.

Abstract

The classification of tropical Indo-Pacific Tectariinae and Echininae (Mollusca: Mesogastropoda: Littorinidae) has been revised. Seven Recent and three Tertiary fossil species belonging to three generic or subgeneric groups are redescribed and figured. Complete systematic synonymies are given, together with discussions of relationships, biology and zoogeography. A list is given of world-wide members of Tectariinae and Echininae.

Introduction

In Part I of Indo-Pacific Littorinidae the species belonging to the subfamily Littorininae were reviewed by Rosewater (1970). The present section covers the subfamilies Tectariinae and Echininae. As yet not covered are such groups as *Bembicium* and its allies and *Cremnoconchus*, although they both occur in the Indo-Pacific region. They are here considered to constitute at least subfamily groups, if not separate families (see Bibliography in Rosewater, *ibid.*, p. 427; Anderson, D. T., 1960, and also Anderson, H., 1958; also see Prashad, 1925 and Kesteven, 1903). The many Antarctic littorinids were excluded from Part I of this study since actually they are out of the geographic area of the tropical Indo-Pacific (see Powell, 1951 and Dell, 1964).

The Littorininae, Tectariinae and Echininae differ in habitat preference and in morphology in a number of aspects. Echininae tend generally to live rather high on the shore. Tectariinae are next and Littorininae usually are nearest to the sea, although considerable variation exists, the genus *Nodilittorina* having some high-living species. The differentiation of the three subfamilies also is based on the following morphological grounds. In Littorininae the radula is of the generalized littorinid type with some narrowing of the central tooth in *Nodilittorina*; opercula are paucispiral; penises are adorned with a few penial glands but otherwise are not particularly complicated.

In the Tectariinae the lateral radula tooth is partitioned and appears thickened and differently oriented than in either Littorininae or Echininae; the opercula are mesospiral (see below); penises are abundantly supplied with glands and are also papillose on non-glandular surfaces. The shells in both Littorininae and Tectariinae usually are imperforate although the subgenus *Ceuchritis* is an exception in the latter subfamily.

In Echininae the radula is not unusual, the subgenus *Tectininus* excepted, where reduction has taken place; opercula are multispiral; shells are umbilicate, usually; penises are supplied with a number of penial glands near the base. In the possession of an umbilicus *Ceuchritis* could be considered to form a bridge between *Tectarius* and *Echininus*. In general, however, *Tectarius* appears to be more closely related to *Littorina* in its conservative characters, while *Echininus* may be considered a specialized group perhaps evolving toward a land environment. These three subfamily groups provide a convenient and apparently natural framework upon which to arrange the contained genera and species (see illus-



Plate 388. Subfamilies Tectariinae and Echininiinae
(explanation on opposite page; all figures about natural size)

trations of these morphological differences in Rosewater, 1970, and in this paper).

Most *Tectarius s.s.* and *Echininus s.s.* are living today only in the East Indian area. With the exception of *Tectarius grandinatus* whose range extends eastward to Polynesia, all other species are inhabitants of the raised, weathered coral reef shorelines found in the Western Pacific Arc (personal observations, 1970). It can only be assumed that this niche provides the requirements essential for the existence of these species as they are to be found nowhere else.

The fossil record provides very few clues to the origin of these groups. There are only three Tertiary fossil species described from the Indo-Pacific and these probably belong in three separate generic taxa. The oldest of these, *T. songoense* Martin, from the Upper Eocene of Java, probably represents nearly the earliest appearance of *Tectarius*. As mentioned in Part I, littorinid fossils are exceedingly difficult to separate from Trochidae and Turbinidae, and this is no less true for *Tectarius* and *Echininus*. Probably, however, these groups made their appearance in the early Tertiary within the region where they have developed, and with the exceptions of *Echininus* (*Tectininus*) *nodulosus* and *Tectarius* (*Cenchritis*) *muricatus*, both of the western Atlantic, they have remained there.

Opercula

The opercula of Indo-Pacific Littorinidae require special comment (see pl. 389). All are made up of conchiolin, and those of members of the subfamily Littorininae, including *Littorina*, its subgenera, and *Nodilittorina* are usually paucispiral and rather oval in shape with the nucleus at the side and nearer one end (oligogyrous spiral type of Fretter, et al., 1962, pp. 79,80). In the Echinininae, the basic plan of the operculum differs from that of other littorines. It is the type

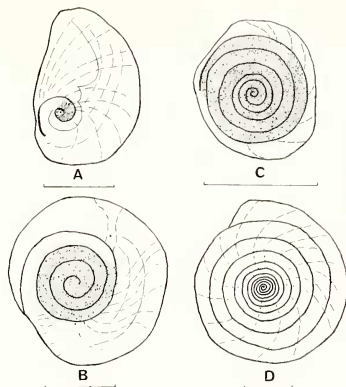


Plate 389. Opercula of Littorinidae and Trochidae.

Fig. A. Paucispiral operculum of *Littorina* (*Littorinopsis*) *scabra* (Linné) from Mokuoloe Id., Kaneohe Bay, Oahu (USNM 339388).

Fig. B. Mesospiral operculum of *Tectarius rusticus* (Philippi) from Troughton Chain, northern Western Australia (WAM 1787-69).

Fig. C. Multispiral operculum of *Echininus cumingi* (Philippi) from near Davao City, Mindanao, Philippines (WAM 1566-70).

Fig. D. Multispiral operculum of *Trochus niloticus* Linné, from Makuluva, Viti Levu, Fiji (USNM 531827). Lines under each figure represent 5 mm.; stippled areas are thickened and dark-brown in color; non-stippled areas are light horn color and transparent.

of operculum which is called in other groups, such as Trochidae, a multispiral operculum (polygyrous spiral type of Fretter, et al., *ibid.*) although not so extreme as that figured by Fretter (*ibid.*, p. 80, fig. 43A; also see our pl. 389, fig. D.). The operculum is circular in outline and moderate to small in size. The nucleus is decidedly central in location and growth proceeds outward from the center in multiple, fairly evenly spaced gyrations (pl. 389, fig. D). The operculum in Tectariinae (fig. B) is intermediate in form between

Explanation to plate 388 (opposite page)

Figs. 1,2. *Tectarius grandinatus* (Gmelin) from Palmerston Atoll, Cook Islands (USNM 685165).

Figs. 3,4. *Tectarius tectumersicium* (Linné). Fig. 3, from Stirling Is., Treasury Is., Solomon Islands (USNM 600370); Fig. 4, from "East Indies" (USNM 131450).

Figs. 5-7. *Tectarius pagodus* (Linné). Fig. 5, from "East Indies" (USNM 18966); Fig. 6, from the Philippines (USNM); Fig. 7, a young specimen from Polillo, Philippines (USNM 311141).

Figs. 8,9. *Tectarius rusticus* (Philippi) from Buccaneer Archipelago, Western Australia (USNM 684713).

Figs. 10,11. *Tectarius rugosus* (Wood). Fig. 10, from Pacific (USNM 304587); Fig. 11, from Davao Bay, Mindanao, Philippines (USNM 654034).

Figs. 12,13. *Echininus cumingi cumingi* (Philippi) from Hervey Is., Cook Is. (USNM 42452).

Figs. 14,15. *Echininus cumingi spinulosus* (Philippi) from Kadena Circle, Okinawa, Ryukyu Is. (USNM 664658).

Figs. 16,17. *Tectarius* (*Cenchritis*) *muricatus* (Linné), from Boca de Camarioca, Matanzas, Cuba (USNM 599944).

Figs. 18-20. *Echininus* (*Tectininus*) *nodulosus* (Pfeiffer). Fig. 18, from Hog Island, Bahamas (USNM 603911); Figs. 19, 20, from Mujeres Harbor, Quintana Roo, Mexico (USNM 662308).

Littorininae and Echininae, being large and rather rounded in outline, with a slightly acentric nucleus and having a number of gyrations more than the paucispiral type but less in number than the multispiral type. The Tectariine opercular type is here termed the mesospiral or mesogyrous spiral type. The presence of the three opercular types in Littorinidae may be considered to have evolutionary significance, and possibly is related to selection for a better aperture sealing mechanism in animals which have considerable vertical distribution on the shore line: in order, proceeding from low toward higher shore habitats—Littorininae, Tectariinae, Echininae.

Reproduction

To my knowledge nothing is known concerning reproduction in either Tectariinae or Echininae with the exception of *Tectarius (Cenchritis) muricatus* (Linné) which produces a pelagic capsule (see Lebour, 1945, and Lewis, 1960, references in Rosewater, 1970 p. 05–276). Field and laboratory studies are needed to discover details of the life histories of the remaining species. However it is likely that most of these snails also produce eggs encased in pelagic capsules which undergo development in the sea. Abbott (1954) noted that Lebour (*ibid.*) stated that some of the Bermuda littorinids that live above high tide line migrate to the water to spawn. It is suspected that this also is the case with many of the Indo-Pacific species.

Acknowledgments

The persons and institutions acknowledged in Part I of this study (see Rosewater, Indo-Pacific Mollusca, vol. 2, no. 11, p. 425) also are thanked here. In addition, I acknowledge the following for their help in making possible the examination in the field of most of the species of *Tectarius* and *Echininus* during the National Geographic Society—Mariel King Memorial Expedition to the Moluccas Islands, Indonesia, May to July 1970: the late Mariel King, Mrs. Grace King, T. H. Richert, C. Beal, C. M. Burgess, B. R. Wilson, and the National Geographic Society. The Government of Indonesia graciously provided clearance for the vessel *Pele* to work in the Moluccas Islands. Mr. Kasim Moosa and Mr. Sukarno, both of the Institute for Marine Research, Djakarta, accompanied the expedition and provided assistance of many kinds.

List of Recognized Taxa

Below is a list of the Tertiary fossil and Recent species herein recognized as belonging in the subfamilies Tectariinae and Echininae. The few fossil taxa are preceded by a dagger [†].

Family Littorinidae Gray, 1840

Subfamily Tectariinae, *new subfamily*

GENUS *Tectarius* Valenciennes, [1832]

Subgenus *Tectarius* Valenciennes, [1832]

rugosus (Wood, 1828). **Type.** Recent, western Pacific

grandinatus (Gmelin, 1791). Recent, Pacific islands

pagodus (Linné, 1758). Recent, western Pacific

tectumpersicum (Linné, 1758). Recent, western Pacific

rusticus (Philippi, 1846). Recent, northern Australia

† *songoense* (K. Martin, 1931). Eocene, Java.

Subgenus

† *Subditotectarius* Ladd, 1966

† *rehderi* Ladd, 1966. **Type.** Miocene, Marshall Islands.

Subgenus *Cenchritis* von Martens, 1900

muricatus (Linne, 1758). **Type.** Recent, tropical western Atlantic.

Subfamily Echininae, *new subfamily*

GENUS *Echininus* Clench and Abbott, 1942

Subgenus *Echininus* Clench and Abbott, 1942

cumingi cumingi (Philippi, 1846). **Type.** Recent, western Pacific

cumingi spinulosus (Philippi, 1847). Recent, western Pacific

† *adelaidensis* (Cotton, 1947). Pliocene, South Australia.

Subgenus *Tectininus* Clench and Abbott, 1942

nodulosus (Pfeiffer, 1839). **Type.** Recent, tropical western Atlantic.

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Key to the Tectariinae and Echiniminae

The following key is to the genera and subgenera of these two subfamilies. It is based upon the shell and externally observable characters. Page numbers are given for Indo-Pacific groups

only, since Western Atlantic taxa are not treated in detail in the present paper. For a key to the Littorininae, see vol. 2, no. 11, p. 430 [p. 05-278].

- 1a Shell umbilicate 2
 1b Shell not umbilicate 3
- 2a Shell spinose, with partially open spines, shell about as wide as high, operculum multispiral (see pl 389) *Echininus* p. 526
 2b Shell not spinose, nodulose, higher than wide, operculum not multispiral . . . *Cenchritis*
- 3a Shell spinose, operculum mesospiral. *Tectarius* p. 513
 3b Shell nodulose, fossil *Subditotectarius* p. 524
 3c Shell moderately spinose, operculum multispiral *Tectininus*

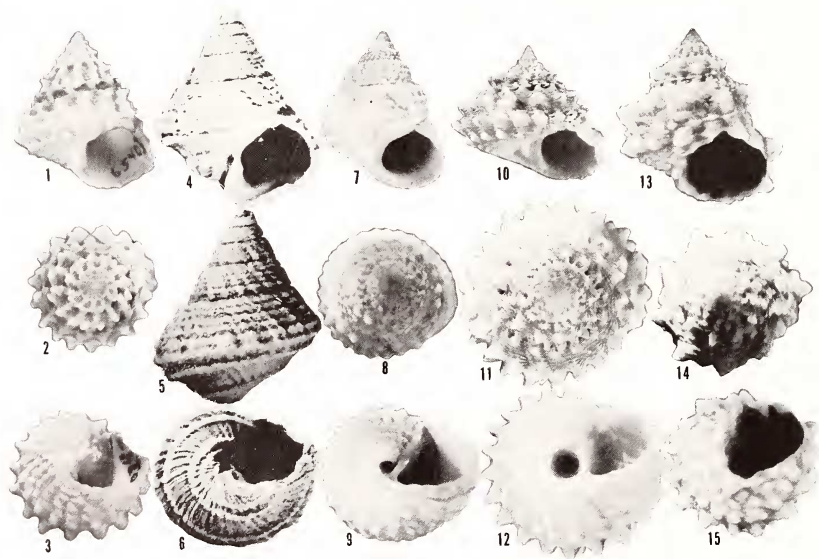


Plate 390. Type-species of Genera and Subgenera of Tectariinae (Figs. 1-9) and Echiniminae (Figs. 10-15) illustrating sculpture, arrangement of spines, and presence or absence of umbilici.

Figs. 1-3. *Tectarius* (*Tectarius*) *rugosus* (Wood), Davao Bay, Mindanao, Philippines (USNM 654034; 23.1 × 17.8 mm.).
 Figs. 4-6. *Tectarius* (*Subditotectarius*) *rehderi* Ladd, early

Miocene, Marshall Islands (Holotype, USNM 648342; 2.8 × 2.4 mm.).

Figs. 7-9. *Tectarius* (*Cenchritis*) *muricatus* (Linné); Matanzas, Cuba (USNM 599944; 26.1 × 17.9 mm.).

Figs. 10-12. *Echininus* (*Echininus*) *comingi* (Philippi); Cook Islands (USNM 42452a; 17.2 × 17.5 mm.).

Figs. 13-15. *Echininus* (*Tectininus*) *nodulosus* (Pfeiffer); Cozumel Id., Mexico (USNM 662806; 14.4 × 12.2 mm.).

Subfamily Tectariinae, new subfamily

Genus *Tectarius* Valenciennes, [1832]

Type: *Tectarius rugosus* (Wood, 1828)

The genus *Tectarius sensu lato* includes the nominate subgenus, *Tectarius*, whose type-species *T. rugosus* Wood (= *T. papillosus* 'Lamarck' of authors) has one of the more conservatively sculptured shells of the group. *Tectarius sensu stricto* is a wholly Indo-Pacific group, having its present population center in the Western Pacific Arc. The monotypic subgenus *Cenchritis* von Martens contains only *T. (C.) muricatus* (Linné), of the tropical western Atlantic (see pl. 388, figs. 16, 17). *Subditotectarius* Ladd, 1966, is monotypic for the fossil *T. (S.) rehderi* Ladd, of the Miocene of the Marshall Islands. Only species belonging to *Tectarius* s.s. and *Subditotectarius* will be considered here.

Tectarius appears more closely related to *Littorina* than to *Echininus* because of greater similarities in morphology, general shell characters, the absence of a truly multispiral operculum, a broader, less modified central radula tooth, and the usual lack of an openly umbilicate shell.

Subgenus *Tectarius sensu stricto*

Moderately large, pyramidal to turbinate, non-umbilicate littorinids with from rather strongly spinose to nodulose or papillose shells; generally living at or above high tide line. Radula littorinoid, the central tooth somewhat narrowed, the lateral tooth with an embayment and usually developing a medial vertical ridge or partition. In males the penis is large and well-supplied with glands along most of its lateral edge, the remainder papillose, and with an open but deeply folded seminal duct. Operculum rounded, mesospiral (see **Opercula** in Introduction). Aperture plicate within; with a columellar swelling or tooth.

Synonymy—

- 1798 *Cidaris* Röding, Museum Boltenianum, part 2, p. 84; type-species by subsequent designation, Hermannsen, 1847: *Trochus pagodus* Linné; non *Cidaris* Leske, 1778, nor Swainson, 1840.

- [1832] *Tectarius* Valenciennes, *Coquilles*, in Humboldt and Bonpland, Voyage aux régions équinoxiales du Nouveau Continent, Observations de Zoologie, vol. 2, p. 271; type-species by subsequent designation Clench and Abbott, 1942: *Trochus coronatus* Valenciennes [= *Tectarius rugosus* (Wood)]. ICZN Opinion 871.
- 1839 *Pagodus* Gray, in *Molluscous Animals: The Zoology of Captain Beechey's Voyage*, p. 141; type-species by Monotypy and by absolute tautonymy, *Monodonta pagodus* Lamarck [= *Tectarius pagodus* (Linné)].
- 1840 *Pagodella* Swainson, A Treatise on Malacology, pp. 207, 219, 221 [refers to *Pagodella echinata*, *nomen nudum*] 351; refers to *P. major* Martini - Chemnitz, pl. 163, figs. 1541, 1542 [= *Tectarius pagodus* (Linné)] and to *T. tectumpersicium* *ibid.*, fig. 1543, 1544; type-species here designated: *Tectarius pagodus* (Linné).
- 1840 *Echinella* Swainson, *ibid.*, pp. 207, 221, 352; refers to *E. granulata* Swainson [nomen nudum] and to *E. coronaria*, Tableau Encyclopédique et Méthodique, pl. 447, fig. 6 [= *Monodonta coronaria* Lamarck = *Tectarius grandinatus* (Gmelin)]; type-species by monotypy, *Tectarius grandinatus* (Gmelin) [also see Clench and Abbott, 1942]; not *Echinella* Bory St. Vincent, 1824.
- 1846 *Fectaria* Philippi, *Abbildungen und Beschreibungen Conchylien*, Vol. 2, *Littorina*, p. 139; used in combination *Fectaria pagodus*; error for *Tectarius* Valenciennes.
- 1858 *Hamus* 'Klein' H. & A. Adams, The Genera of Recent Mollusca, vol. 2, p. 656, refers to H. and A. Adams, 1854, vol. 1, p. 315; type-species here designated, *Hamus pagodus* (Linné) [= *Tectarius pagodus* (Linné)]; not *Hamus* 'Klein' R. B. Watson, 1886 [= Trochidae].
- 1899 *Echnellops* Rovereto, Atti della Società Ligustica di Scienze naturali e geografiche, vol. 10, p. 109; new name for *Echinella* Swainson, 1840, not Bory St. Vincent, 1824.

Nomenclature—Due to similarities between the shells of *Tectarius* and some of the Trochidae, there has been a tendency for some of the former to be classified with the latter. This problem was discussed by Keen (1966) who recommended that the International Commission on Zoological Nomenclature validate *Tectarius* with the type-species *Tectarius coronatus* Valenciennes, [1832], i.e., in its accustomed sense. Her petition was granted in I.C.Z.N. Opinion 871 (Melville and China, 1969). It was assumed in this Opinion that the type-species of *Tectarius*, *T. coronatus* Valenciennes, is a synonym of *T. grandinatus* Gmelin. However, an examination of the type-specimen of *coronatus* in the Paris Museum shows it to be in actuality *T. rugosus* Wood, which usually has been erroneously referred to as *T. papillosus* Lamarck.

Another name which sometimes has been associated with *Tectarius* that has an exceedingly long and complicated history is the genus *Hamus*. It was mentioned originally by Klein (1753) where its use was of course pre-Linnaean. Bruguière (1792) gave a brief description, referring to Klein, but listed no species. Deshayes (1830)

declared it "a forgotten genus", indicating that he considered it unrecognizable. Mörch (1852) listed it, this time in the synonymy of *Littorina* Férussac, an invalid introduction (I.C.Z.N., Art. 11(d)). The first valid use of *Hamus* was not until H. & A. Adams (1858) used it as a senior synonym for *Tectarius* (see synonymy). It was later used by Wimmer (1880) and Watson (1886), the last being a taxon of Trochidae. I have designated as type-species of *Hamus* H. and A. Adams, 1858, *H. pagodus* (Linné) and consider this genus to be an absolute synonym of *Tectarius* Valenciennes.

The use of square brackets surrounding the date for *Tectarius* Valenciennes, [1832] is recommended by the International Code of Zoological Nomenclature in cases where the date of publication of a name has been determined on the basis of external evidence (I.C.Z.N. Recommendation 22A(3); also see Sherborn and Woodward, 1901; Keen, 1966; and Opinion 871).

***Tectarius rugosus* (Wood, 1828)**

(Pl. 388, figs. 10, 11)

Range—Philippines and Indonesia.

Remarks—The shells of well prepared and cleaned specimens of *Tectarius rugosus* tend to be quite colorful for Littorinidae, with the orange-pink coloration of the last two whorls contrasting with a purplish brown subsutural band. These colors do not show well in all specimens, however, and are not very visible in uncleaned specimens. The three large, non-umbilicate common species of the southwest Pacific may be distinguished by the number of major spiral rows of spines on the last whorl: 2 in *pagodus*; 3 in *tectumpersicum*; and 4 in *rugosus*. The closely-spaced stubby spines of *rugosus* also separate it from the other two. These characteristics do not of course help to distinguish it from *T. grandinatus*, but other characters and the Polynesian endemicity of the latter are helpful in this case (see *Remarks* under *grandinatus*).

Habitat—Shore rocks and limestone cliffs 1-2 meters above high tide line (personal observations, Davao, Philippines, 1970).

Description—Shell reaching 39.7 mm (about 1½ inches) in length, broadly conical in shape, average obesity about .76 (51 specimens range from .68-.82); mature specimens moderately heavily constructed, imperforate, and sculptured on most postnuclear whorls with four, fairly closely-spaced rows of stubby, rounded, often slightly upturned spines. External color generally

yellowish white on early whorls, becoming pinkish orange on penultimate and body whorls; area of most posterior (subsutural) row of spines usually a contrasting purplish brown, and the same dark color may appear in lines and dashes inside outer lip of aperture; aperture tinted lighter pinkish orange. Base flattened, sculptured spirally with nodulose cords, a larger separate row just below periphery of body whorl. Whorls 6-8, flat-sided excepting spines. Length of spire usually greater than half the length of shell. Spire convex, produced at an angle of from about 60-67°. Aperture rounded-squarish; outer lip thickly produced in mature individuals, strongly plicate within; plicae not reaching edge of aperture; outer lip tapering to a thin, crenulate edge; inner lip smooth posteriorly, often stained a deeper orange than rest of aperture, forming a tooth-like bulge anteriorly, near junction with outer lip near base of columella. Suture obscured by anteriormost row of spines of preceding whorl. Primary sculptural feature is the four spiral rows of spines. Spines not particularly aligned axially, although anteriormost 2 rows more so than others; from 17-23 spines per row on body whorl; bases of anteriormost 3 rows of spines joined by low spiral carinae. Posterior-most-but-one (3rd) row of

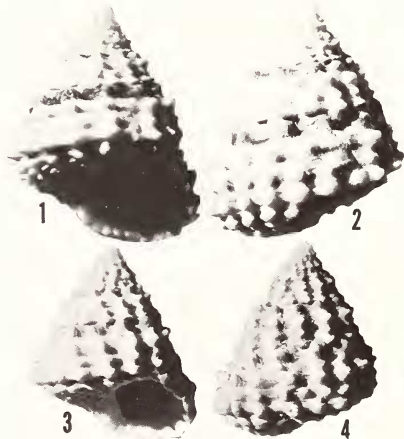


Plate 391. *Tectarius rugosus* (Wood, 1828).

Figs. 1,2. *Turbo rugosus* Wood, lectotype, BM(NH) 1968370, 28.4 × 22.3 mm.

Figs. 3,4. *Tectarius coronatus* Valenciennes, Holotype, MHNP ("Acapulco") [Luzon, Philippines] 32.9 × 25.7 mm.

spines protrudes farthest on spire whorls, but this distinction largely lost on more mature whorls; posteriormost (4th) row of spines obscured by subsutural purplish brown color band especially on penultimate and body whorls. Secondary spiral sculpture, between each row of spines, consisting of raised cords, and overall spiral sculpture of microscopic threads. Axial sculpture consists of irregular flaky lines of growth. Operculum moderate in size, circular, an average one measuring about 7 mm. in diameter, thin, light-brown with a dark-brown center, paucispiral, nucleus about central. Periostracum not evident. Nuclear whorls at least partially decollate in all specimens examined, about 2, smooth, grayish white, first postnuclear whorls showing early signs of spiral striae and becoming nodulose. Radula littorinoid, 2-1-1-1-2; lateral tooth with a vertical partition and an embayment typical of Littorinidae. Animal moderately large, littorinoid; penis large, muscular and apparently highly extensible; seminal groove in deep fold running along medial edge to tip; tip vermiform, covered with papillae; lateral edge of penis supplied with large number of glands not extending onto vermiform tip. Reproductive data and life history unknown.

Measurements (mm) (all Philippiines)—

length	width	No. whorls	locality
39.7	27.6	7+	Cadao Id., Naro Bay, Masbate
35.4	25.2	7+	Cadao Id., Naro Bay, Masbate
30.1	22.4	7+	San Miguel Bay, Ticao
25.9	21.2	8	Batag Id., Samar
23.9	16.3	7+	Bongao Channal, SW Sanga Sanga Id., Sulu Archipelago
21.0	15.3	7+	Borongan, E side Samar
17.5	13.7	7+	Papahag Id., Tawi Tawi Group
15.0	12.0	6+	Borongan Village, E side Samar
13.5	10.8	7+	Papahag Id., Tawi Tawi Group
12.6	9.8	6+	Papahag Id., Tawi Tawi
11.2	8.4	6+	Papahag Id., Tawi Tawi
8.4	6.8	5+	Papahag Id., Tawi Tawi

Synonymy—

- *Monodonta papillosa* of authors, not *M. papillosa* Lamarck, 1822 [= *Tectarius tectumpersicum* (Linné, 1758)].
- 1828 *Trochus rugosus* Wood, Supplement to the Index Testacologicus or a Catalogue of Shells, British and Foreign, pl. 5, *Trochus*, fig. 7 (no locality given; Mindanao, Philippines, here selected; lectotype in BM(NH) 1968370, length 28.4 mm, width (ca.) 22.3; not *Litorina rugosa* Menke, 1843 [= *Nodilittorina australis* (Gray, 1826)].
- 1832 *Tectarius coronatus* Valenciennes in Humboldt and Bonpland, Voyage aux régions équinoxiales du Nouveau Continent, vol. 2, *Coquilles*, p. 271 (Acapulco [in error] locality here corrected to Luzon, Philippines); Holotype in MHNP.

1846 *Litorina papillosa elegans* Philippi, Abbildungen und Beschreibungen Conchylien, vol. 2, p. 140, *Litorina*, pl. 2, figs. 5, 7 (precise locality not given); figured specimens from Cuming Collection BM(NH) [not seen during 1968 visit] and Saul Collection, Cambridge Museum.

1846 *Litorina papillosa quadriseriata* Philippi, *ibid.*, p. 140, *Litorina*, pl. 2, fig. 2 (Zanzibar [in error] locality here corrected to Luzon, Philippines); type-specimen may be in BM(NH) [not seen during 1968 visit]; refers to "*Trochus rugosus* Wood Suppl. t.5, l. 7".

Types—Although the name *T. papillosus* has been applied to this species (see Kaicher, 1956) the type-specimen of that species in the Geneva Museum is unquestionably *T. tectumpersicum* Linné, and *papillosus* is, therefore an absolute synonym of *tectumpersicum* (q.v.). It also has been referred to as *Echinellopsis grandinatus* (Habe, 1961, p. 20; 1964, p. 28, both pl. 9, fig. 30) which is an error of nomenclature for *T. rugosus*. The first available name is *Trochus rugosus* Wood, 1828, the lectotype of which is in the BM(NH) 1968370. The holotype of *T. coronatus* Valenciennes is in the Paris Museum. The figured specimens of Philippi's *elegans* and *quadriseriata* may be in the BM(NH) and/or the Cambridge Museum. They were not discovered by me at the BM and may be lost. Philippi's figures are quite adequate for the interpretation of the species and may be considered as representative of the lectotypes: *elegans*, pl. 2, fig. 7; *quadriseriata*, pl. 2, fig. 2.

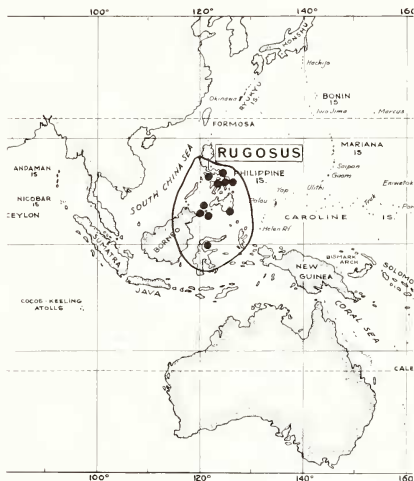


Plate 392. Geographic distribution of *Tectarius rugosus* (Wood) in the Philippines and Indonesia.

Records—PHILIPPINES: Port Galera, Mindoro; San Miguel Bay, Ticao Id.; Cadao Id., Naro Bay, Masbate (all USNM); Borongan Village (USNM, Del. Mus. N.H., ANSP, MCZ); Batag Id., both Samar (USNM); Samal Id., Davao Bay (MCZ, USNM, WAM); Zamboanga, both Mindanao (ANSP, Del. Mus., N.H.); Jolo Id. (MCZ); Tabawan Id. (ANSP); Papahag Id. (USNM); Bongao Channel, SW Sanga Sanga Id., all Sulu Archipelago (ANSP). INDONESIA: Buka Buka Id., Gulf of Tomini, Celebes (USNM).

***Tectarius grandinatus* (Gmelin, 1791)**

(Pl. 388, figs. 1,2; pls. 393-395)

Range—The Cook, Society, Tuamotu and Gambier Islands, southeastern Polynesia.

Remarks—*Tectarius grandinatus*, an inhabitant of southeastern Polynesia, apparently is geographically isolated from the several other members of the genus *Tectarius* in the Indo-Pacific, the others being found in the East Indies. It is quite distinct, morphologically, from *pagodus* and *tectumpersicum*, but, interestingly, is very close in appearance to *T. rugosus* in general matters of sculpture and external anatomy of the animal. Superficially, *grandinatus* might be thought more closely related to *Cenchritis muricatus* (L.) of the western Atlantic. However, the radula, penial anatomy (Abbott, 1954) and a close examination of shell sculpture and structure causes me to reject that theory: *grandinatus* has not been observed to be umbilicate, while *muricatus* sometimes is; the aperture of *muricatus* is never thickened and plicate as it is in *grandinatus*; the operculum of *grandinatus* is rounded with the nucleus near the center, that of *muricatus* is more oval with the nucleus near the side.

The many similarities between *rugosus* and *grandinatus* together with their spatial isolation suggest the possibility that they may have evolved from the same species stock. Although a subspecific relationship may be indicated, the two are here considered to have developed full specific differentiation.

Habitat—Usually occurs on low islands within the geographic range; on coral reef flats near the high tide line, on jagged pieces of raised reef.

Description—Shell reaching 37.9 mm (about 1 1/2 inches) in length, elongate conical in shape, average obesity about .72 (44 specimens range from .62-.82); rather solidly and thickly constructed for its size, imperforate; mature specimens with very deeply impressed suture and rounded whorls; sculptured with four spiral rows per whorl of stubby spines. External shell color yellowish white; often coated with what appears

to be a light-yellow to brown or rather dark grayish brown periostracum which may wear thin especially at tips of spines; no definite color pattern apparent; occasional lines or splotches of medium brown present; upper (most posterior) part of aperture usually covered with a brown glaze. Base moderately flattened, sculptured spirally with nodulose cords. Whorls 7-9, moderately rounded. Length of spire usually considerably greater than half the length of shell. Spire convex, produced at an angle of from 58-60°. Aperture rounded; outer lip considerably thickened, plicate within, tapering to a thinner, crenulate edge. Inner lip with a thin, brown glaze posteriorly, forming a tooth-like bulge anteriorly, near junction with outer lip near base of columella. Suture often deeply impressed, typically forming a channel between whorls. Primary sculptural feature is the four spiral rows of spines. Spines not regularly aligned axially, although anteriormost two rows more-so than others; from about 17-25 spines per row on body whorl; bases of anteriormost 3 rows of spines joined by low spiral carinae; bases of posteriormost row of spines usually separate; second from anterior row usually the smallest. Secondary spiral sculpture be-



Plate 393. *Tectarius grandinatus* (Gmelin, 1791).

Figs. 1,2. *Trochus grandinatus* Gmelin, lectotype in ZMC, specimen figured by Chemnitz, Conchylien Cabinet, vol. 10, pl. 169, fig. 1639, from Palmerston Atoll, Cook Islands, 32 × 22.4 mm.

Figs. 3-5. *Monodonta coronaria* Lamarck, holotype, MHNG 1096/23, 41 × 27 mm.

tween rows of spines consisting of 2-4 raised cords; overall microscopic sculpture of fine, closely-spaced spiral threads. Axial sculpture consisting of fine, irregular, closely-spaced, overlapping lines of growth. Shell surface under high magnification may show minute closely-spaced perforations. Operculum moderate in size, rounded-oval, an average one measuring about 9 mm. in diameter, thin, light-brown with a dark-brown center, paucispiral, nucleus about central. A thin, light- to dark-brown periostracum present; closely applied but easily worn away; periostracum smooth and dully shining. Nuclear whorls about $1\frac{1}{2}$, smooth and shining; first post-nuclear whorl rapidly becoming multi-carinate and developing spines on the second. Radula littorinoid, 2-1-1-2; lateral tooth with a vertical partition and with an embayment characteristic of Littorinidae. Animal moderately large, littorinoid. Penis fairly large and apparently quite extensible; seminal groove in deep fold running along medial edge to tip and bordered by thickened, papillose glandular-appearing tissue; distal end of penis vermiform; lateral edge of penis lined with large number of glands not extending onto vermiform tip. Reproductive data and life history unknown.

Measurements (mm)—

length	width	no. whorls	locality
37.9	23.4	7+	Manihi, Tuamotu Ids.
34.3	21.5	7+	Aitutaki, Cook Ids.
32.0	22.8	6+	Mangaia, Cook Ids.
29.8	21.2	7+	Mangareva, Gambier Ids.
24.3	18.7	8+	Bird Id., Palmerston Atoll
22.0	17.0	9	Bird Id., Palmerston Atoll
20.7	15.7	7+	Cooks Motu, Palmerston Atoll
18.1	14.7	7+	Mangaia, Cook Ids.
16.1	13.2	6+	Aitutaki, Cook Ids.
14.3	10.8	6+	Aitutaki, Cook Ids.
12.4	9.1	9	Tikahau Atoll, Tuamotu Ids.
7.8	6.0	6+	Mangaia, Cook Ids.

Synonymy—

- [1784] *Trochus bullatus* Martyn, The Universal Conchologist, vol. 1, fig. 38; rejected work, I.C.Z.N. Opinion 456].
 1791 *Trochus grandinatus* Gmelin, Systema Naturae, ed. 13, p. 3585 (ad Palmerstoni insulam [= Palmerston Atoll, Cook Islands]; refers to Chemnitz "Conch" vol. 10, p. 291, pl. 169, fig. 1639 and to Martyn "Conch", vol. 1, fig. 38. Lectotype, here selected, specimen from Spengler Collection, ZMC, figured by Chemnitz; see our pl. 393, figs. 1 and 2, 32×22.4 mm).
 1816 *Monodonta coronaria* Lamarck, Liste Des Objets Représentés, Tableau Encyclopédique et Méthodique, part 23, p. 10, pl. 447, fig. 6 a,b (no locality given); Holotype MHNG 1096/23, 41×27 mm; 1822, Histoire Naturelle Des Animaux sans Vertèbres, vol. 7, p. 33.

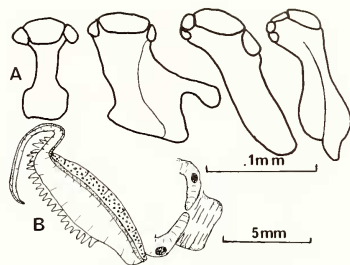


Plate 394. *Tectarius grandinatus* (Gmelin).

Fig. A. Radula.

Fig. B. Penis (both from Palmerston Atoll, Cook Islands, USNM 685165).

Types—The lectotype of *Trochus grandinatus* Gmelin, the specimen figured by Chemnitz, vol. 10, p. 291, pl. 169, fig. 1639, is in the Zoological Museum Copenhagen. It measures 32×22.4 mm (see pl. 393, figs. 1,2). The Holotype of *Monodonta coronaria* Lamarck is in the MHNG 1096/23 (see pl. 393, figs. 3-5). It measures 41×27 mm.

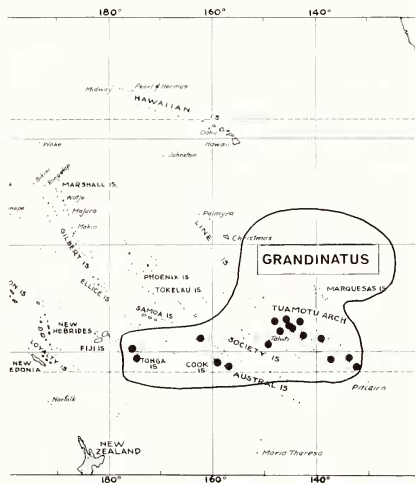


Plate 395. Geographic distribution of *Tectarius grandinatus* (Gmelin) in the southeastern Pacific Ocean.

Records—COOK ISLANDS: Palmerston Id.; Aitutaki (both USNM, ANSP, Del. Mus. N.H.); Hervey Ids. (USNM, MCZ, ANSP); E. side Koromiri Id.; S.E. Rarotonga (ANSP); Mangaia (USNM). SOCIETY ISLANDS: W. coast Bora Bora (ANSP); Tahiti (USNM, MCZ, ANSP). TUAMOTU ISLANDS: Manihi Atoll (USNM); Takaroa Atoll (ANSP); Maiaï Id., Tikehau Atoll (USNM); Aratika Atoll (ANSP); N. of Temao Harbor, Makatea Id. (USNM); Toan Atoll; Raroia Atoll; (all ANSP) Raraka Atoll (Del. Mus. N.H.); Fakarava Atoll; Makemo Atoll; Tatakoto Atoll; Anaa Atoll; Vahitahi Atoll; Nengonengo Atoll; Tureia Atoll (all USNM); Marutea Atoll, Acteon Group (ZMA). GAMBIE ISLANDS: Mangareva Id. (USNM, MCZ).

Tectarius pagodus (Linné, 1758)

(Pl. 388, figs. 5-7)

Range—From the Philippines, through the Western Pacific Arc to the Solomon Islands.

Remarks—The name applied by Linné to this species could not have been more appropriately descriptive as the shell with its usually upturned spines very much resembles an oriental turreted pagoda. As pointed out by Dodge (1959) there are a number of similarities between *T. pagodus* and *T. tectumpersicum*, both described by Linné. However *pagodus* reaches a larger size, $2\frac{1}{2}$ inches versus 1 inch, is proportionately broader and has more prominent spinose carinae than *tectumpersicum*. There is seldom any difficulty in separating these species with comparative material at hand.

The method of reproduction in *pagodus* remains to be observed. The normal habitat of the species is on cliffs above the sea. As there is no evidence that the species is ovoviviparous, there must be a periodic migration to the sea for breeding purposes, although such a phenomenon has not been reported.

Another question arising from the high shore habitat of these nominally marine snails concerns their food. Rumphius (1705) early suggested that they feed upon the cliffs where they live. Examination of some fecal pellets of this species revealed the presence of considerable debris and what appeared to be plant cells. It is quite likely that *T. pagodus* feeds on plant life such as algae and lichens growing on the sea cliffs. The radula is extremely long which may denote such a browsing manner of feeding, the extra length possibly being required because aerial feeding without lubrication from sea water causes a rapid wearing of the teeth (see Quoy and Gaimard, Astrolabe, pl. 62, fig. 1).

Habitat—"... these animals suck their food from the briny moisture of the cliffs to which they

cling, being unable to endure the water" (Rumphius, 1705, p. 74). Found on vertical limestone cliffs 1-2 meters above high tide line (personal observations, Moluccas Islands, Indonesia, 1970).

Description—Shell reaching 61.4 mm. (about $2\frac{1}{2}$ inches) in length, squatly conical in shape, average obesity about .93 (18 specimens range from .84-1.1); mature individuals rather heavily constructed, imperforate, and sculptured on the body whorl with 2 carinate rows of usually thick, straightly projecting or slightly upturned spines, between which spiral cords are roughly produced and the shell surface often thrown into oblique waves. Overall external color yellowish to grayish white, with no discernable pattern; in young specimens dark-brown spiral lines may be present externally or within aperture; aperture usually yellowish brown, its edge white. Base distinctly flattened, sculptured spirally with nodulose cords extending into aperture; base separated from upper part of body whorl by one of the rows of spines at periphery. Whorls 5-8, flat-sided, excepting spines. Length of spire usually greater than half the length of shell. Spire convex, produced at an angle, excepting spines, of from 55-65°. Aperture broadly rounded; outer lip thickly produced in mature individuals, strongly plicate within; plicae not reaching edge of aperture; inner lip smooth, white posteriorly, but forming a prominent tooth-like bulge anteriorly near junction with outer lip at base of columella. Suture somewhat obscure, marked by protrusion of secondary carinae of succeeding whorl. Outstanding sculptural feature is the midwhorl spinose carina, with typically from 9-12 antero-posteriorly flattened, triangularly-shaped spines on carina of body whorl. Surface of shell at base of spines raised to form oblique fold often reaching to suture. Secondary spine bearing carinae at per-



Plate 396. *Tectarius pagodus* (Linné, 1758).

Fig. 1. *Turbo pagodus* Linné; lectotype figure from Argenville, pl. 11, fig. a.

Figs. 2, 3. *Monodonta bicolor* Lamarck, holotype, MHNG 1096/19, 54 × 38.2 mm.

iphery of each whorl, entirely visible only on body whorl and protruding above suture of preceding whorls. Secondary spiral sculpture of raised, roughened spiral cords in turn, covered with countless closely-spaced spiral microscopic textural threads. Operculum large (average about 16 mm. diameter) thin, brown, circular, corneous, paucispiral, nucleus about central. Periostracum not evident. Nuclear whorls partially decollate in all specimens examined, earliest whorl (probably first postnuclear) is spirally striate, the midwhorl carina beginning about second postnuclear whorl; carina becoming nodulose or prespinose almost immediately. Radula littorinoid (2-1-1-1-2) extremely long; lateral tooth partitioned and with an embayment. Animal large, also littorinoid; sides of foot and tentacles bright yellowish orange, remainder of animal grayish brown (color observations on living animals from Kai Islands, Moluccas, Indonesia); penis well-developed, with the seminal duct contained within a deep fold running along its medial edge; with a large number of glands attached along lateral edge; penis minutely papillose also over its surface, unbranched. Reproductive data and life history unknown.

Measurements (mm) (width includes spines)

length	width	no. whorls	locality
61.4	45.0	7+	Lutee, Choiseul Id. Solomon Islands
57.1	47.8	6+	Pavuvu Id., Russel Group, Solomon Islands
49.3	42.3	7+	Lutee, Choiseul Id. Solomon Islands
46.9	43.4	8+	Pavuvu Id., Russel Group, Solomon Islands
44.4	42.3	7+	Bougainville Id., Solomon Islands
41.3	37.4	5+	Majugat Id., W coast Buka Id., Solomon Islands
39.7	40.0	8	Lutee, Choiseul Id., Solomon Islands
31.5	31.9	6+	Balagnan Id., Surigao District, Mindanao, Philippines
27.5	25.5	8	Socepori Ids., Schouten Ids., West Irian
14.3	12.6	7	Biak, West Irian

Synonymy—

- 1758 *Turbo pagodus* Linné, *Systema Naturae*, ed. 10, p. 762; refers to Argenville, pl. 14, fig. A "Pagodus" [lectotype figure]; (type-locality, O. Asiatico, here restricted to Amboina, Moluccas).
- 1822 *Monodonta bicolor* Lamarck, *Animaux sans Vertèbres*, vol. 7, p. 31 (no locality); holotype in MHNG 1096/19, 54 × 38.2 mm.

1840 *Pagodella major* Swainson, *A Treatise on Malacology*, p. 351 (no locality given); refers to Chemnitz, pl. 163, figs. 1541, 1542 (specimen figured is lectotype, possibly in Copenhagen Museum).

1850 *Pagodus* versus J. E. Gray in M. E. Gray, *Figures of Molluscan Animals*, vol. 4, p. 78; refers to *Trochus pagodus* Quoy [and Gaimard, *Astrolabe*] pl. [62, not "82"], figs. 1-4; not *Littorina papillosa* var. *vera* Philippi, 1846 [= *Tectarius tectumpersicum* Linné].

Types—The location of Linné's type of *Turbo pagodus* is unknown, and Dance (1967) has pointed out that this species is missing from the Linnaean collection in London. In the absence of a type, one of the figures cited by Linné in connection with the original description is here

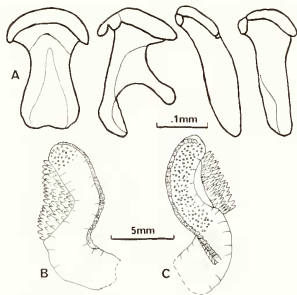


Plate 397. *Tectarius pagodus* (Linné).

Fig. A. Radula of specimen from West Irian; note smooth cusps probably denoting worn teeth, also "partitioned" lateral.

Fig. B. Penis, anterior, and C. posterior views respectively; note glands on lateral edge and papillose surface (both ANSP 207638).

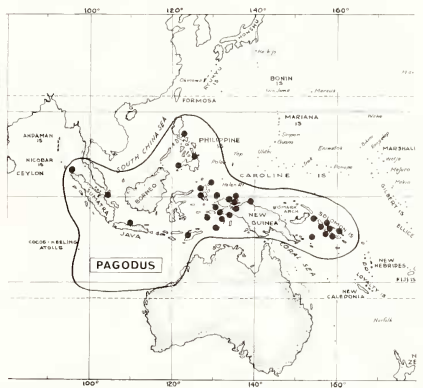


Plate 398. Geographic distribution of *Tectarius pagodus* (Linné) in the central Indo-Pacific faunal region.

designated as representing the lectotype: Argenville, pl. 11, fig. A. The type-locality, originally given as "O. Asiatico" is here restricted to Amboina, Moluccas. The holotype of *Monodonta bicolor* Lamarck is in the Museum d'Histoire Naturelle, Geneva (MHNG register no. 1096/19). The location of types of Swainson's *Pagodella major* and of Gray's *Pagodus verus* are unknown to me, and the figures cited in connection with their descriptions may be considered as representing their lectotypes (see *Synonymy*).

Records—PHILIPPINES: E. coast Polillo (Del. Mus. N.H., USNM); Calapan, Mindoro Id. (Del. Mus. N.H.); Balagnan Id., Surigao District (USNM); Zamboanga, both Mindanao (ANSP, Del. Mus. N.H.). INDONESIA: Pulau We, Sumatra (RNHL); Java (ANSP, RNHL); Timor (RNHL); Morotai Id.; Toctoe Id.; Dagsaseli, both N Loloda Group (all MCZ); Ternate (RNHL); Buru Id. (ZMA); Ambon (MCZ, ZMA); Tanimbar Islands (RNHL); Kur Id.; Warbal Id., W of Nuhu Rowa, both Kai Ids. (both USNM, WAM). NEW GUINEA: Waigeo Id. (ANSP); Misool Id.; Fakfak (both Leiden); Manokwari (ANSP); Biak; Soepiori Id., both Schouten Ids. (both USNM); Ronw, Aoceri Ids. (ANSP); Woodlark Id. (MCZ). SOLOMON ISLANDS: Majugag Id., W coast Buka Id.; Nr. Kihili, Buin, Bougainville Id. (both USNM); Choiseul Bay (ANSP); Lutee, both Choiseul Id. (ANSP, USNM); Ataa District, Malaita (ANSP); Roviana (MCZ); Pavuvu, Russell Group (USNM).

Tectarius tectumpersicum (Linné, 1758)

(Pl. 388, figs. 3,4)

Range—From the Philippines along the West-ern Pacific Arc through Melanesia.

Remarks—*Tectarius tectumpersicum* is grossly similar in many ways to *T. pagodus* and it often appears difficult to construct a point by point comparative description which clearly differentiates the two species except in matters of size and degree of obesity; *pagodus* reaches a length of 2½ inches (61 mm) while *tectumpersicum* rarely reaches 1½ inches (34 mm); *pagodus* is very obese, sometimes being wider than high, but in *tectumpersicum* the width of shell is generally only about 77% of the length. Differences are apparent also in spinosity, there being two rows of spines on the body whorl of *pagodus* and 3 rows in *tectumpersicum*. Spines in *tectumpersicum* tend to be stubby and round-ended while in *pagodus* they are pointed and broadly triangular, although there are occasional specimens of *tectumpersicum* which tend to resemble small, mature *pagodus*. Generally, however, specimens of *pagodus* the size of *tectumpersicum* are obviously immature and thin-lipped, so that the "rule-of-thumb" involving size of specimens can be depended on to separate the species.

Habitat—Lives in pockets of worn, raised limestone reef rock, 1-2 meters above high tide line (personal observations, Moluccas Islands, Indonesia, 1970).

Description—Shell reaching 34.6 mm (about 1⅞ inches) in length, conical in shape, average obesity about .77 (38 specimens range from .64-.85), mature individuals moderately thick in structure, imperforate, and sculptured with three main rows of stubby, often upturned, spines on body whorl, and usually with two rows on spire whorls, between which spiral cords are roughly produced, wavy or papillose and often approaching minor rows of spines. External color yellowish to grayish white, with no regular patterning although some specimens have diffuse dark spiral color bands externally or within aperture especially at edge of outer lip or on tooth-like bulge of inner lip. Remainder of aperture usually white or yellowish white. Base moderately flattened,

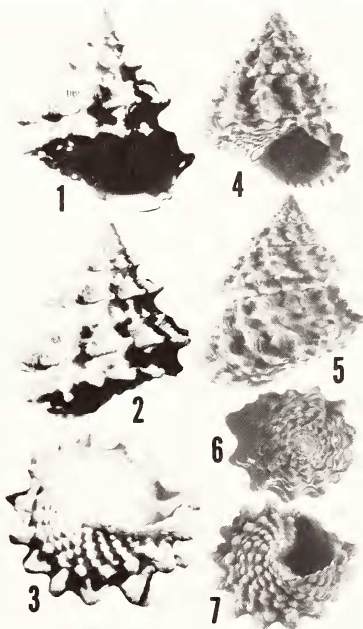


Plate. 399. *Tectarius tectumpersicum* (Linné, 1758).

Figs. 1-3. *Turbo tectumpersicum* Linné, lectotype in Linnean Society of London collection, ca. 25 × 23 mm.

Figs. 4-7. *Monodonta papillosa* Lamarck, lectotype, MHNG 1096/22-2, 29.3 × 25.5 mm.

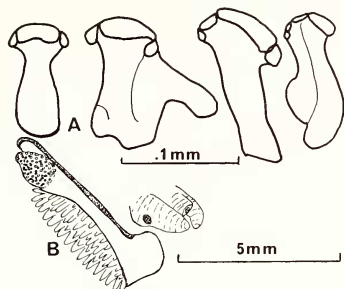
Plate 400. *Tectarius tectumpersicum* (Linné).

Fig. A. Radula.

Fig. B. Penis (both from Biak, West Irian, ANSP 206421 and USNM 637390).

sculptured spirally with nodulose cords which may extend into aperture; base separated from upper part of body whorl by a row of spines at periphery. Whorls 6-8, rather flatsided excepting spines. Length of spire greater than half the length of shell. Spire convex, produced at an angle of from about 55-65°. Aperture compactly rounded; outer lip thickly produced; strongly plicate within, but thin and crenulate at apertural edge; inner lip smooth posteriorly, but forming a tooth-like bulge anteriorly near junction with outer lip at base of columella. Suture obscure, partially masked by lower row of spines at periphery of whorls. Center row usually bearing largest spines, from 9-12 on body whorl; the more posterior row, near suture has smaller spines but about same number; anterior row at periphery smaller still and more numerous with from 13-16 spines. On spire whorls center row of spines may predominate with others being either hidden or suppressed. Spines usually not aligned axially. Secondary spiral cords in some specimens almost as spinose as primary ones; in other specimens hardly noticeable. Entire surface covered with closely spaced spiral microscopic textural threads. Axial sculpture consists of often coarse, irregular lines of growth. Operculum moderate in size (average about 6-7 mm diameter), thin, brown, circular, corneous, paucispiral, nucleus about central. Periostracum not evident. Nuclear whorls about two, but at least partially decollate in all specimens examined; brown, smooth for at least 1 volution, then becoming carinate; first post nuclear whorl weakly nodulose and rapidly becoming spinose. Radula littorinoid (2-1-1-1-2)

[teeth about $\frac{1}{2}$ the size of those of *T. pagodus*]; lateral tooth partitioned and with an embayment. Animal medium-sized, littorinoid; penis large, unbranched, with a large number of glands along lateral edge, $\frac{3}{4}$ the length to tip; surface of penis otherwise papillose; seminal duct deeply folded. Life history unknown.

Measurements (mm) (width includes spines)—

length	width	no. whorls	locality
34.6	24.5	6+	Pavuvu Id., Russell Group, Solomon Islands
31.4	23.3	8	Lunga, Guadalcanal, Solomon Islands
26.7	17.4	7+	Timor, Indonesia
22.8	18.4	6+	Cebu, Philippines
21.4	15.9	7+	Biak, West Irian
20.0	15.5	6+	Biak, West Irian
19.2	16.0	6+	Cebu, Philippines
18.1	13.7	7+	Biak, West Irian
15.2	12.9	6+	Anir Id., New Ireland
13.6	10.3	8	Philippines

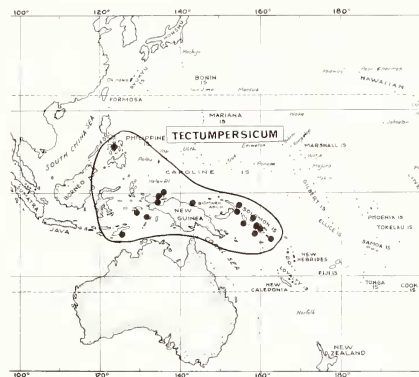
Synonymy—

1758 *Turbo tectumpersicum* Linné, Systema Naturae, ed. 10, p. 762 (no locality given; Cebu Id., Philippines, here selected as type-locality); lectotype in Linnean Society of London collection.

— *Trochus bullatus* "Martyn" of authors; [not *T. bullatus* Martyn, 1784, Universal Conchologist, vol. 1, fig. 38; non-binomial; is *Tectarius grandinatus* (Gmelin, 1791)].

1822 *Monodonta papillosa* Lamarck, Histoire Naturelle des Animaux sans Vertèbres, vol. 7, p. 32, ("les mers de Timor"); lectotype MHNG 1096/22-2.

1846 *Litorina papillosa vera* Philippi, Abbildungen und Beschreibungen Conchylien, vol. 2, p. 141 (no locality given); refers to "Desessert, Recueil, pl. 36, fig. 10," here selected as the lectotype figure.

Plate 401. Geographic distribution of *Tectarius tectumpersicum* (Linné) in the central Indo-Pacific faunal region.

Types—The specimen of *Turbo tectumpersicum* Linné in the Linnaean shell collection located in the Linnaean Society, London, may be considered the lectotype of this species; it measures approximately 25mm length (about 1 inch). The lectotype somewhat resembles *T. pagodus* but may be recognized by its rounded spines and the mature, thickened shell. The figure cited by Linné, "Argenville, pl. 11, fig. P", is controversial and a poor representation of the species (also see Dodge, 1959, p. 229). As no type-locality was given by Linné, Cebu Island, Philippines, is here selected as a place from which specimens could have come in the early 18th century. The figure referred to by Philippi, "Delessert, Recueil, pl. 36, fig. 10", is here selected as the lectotype figure of *Litorina papillosa vera*. The lectotype of *Monodonta papillosa* Lamarck, which proves to be an absolute synonym of *T. tectumpersicum* is in the Geneva Museum (MHNG 1096/22-2; see our pl. 399 figs. 4-7).

Nomenclature—The name *tectumpersicum* does not need to agree in gender with *Tectarius* because the former is a noun in apposition, meaning "persian roof".

Records—PHILIPPINES: Cebu (USNM). INDONESIA: Timor (USNM, RNHL); Ambon; Kur Id.; Warbal Id.; W of Nulu Rova; both Kai Islands (all USNM, WAM). NEW GUINEA: Wasior, Wandammen Bay (ZMA); Soepiori Id. (MCZ); Biak Id., both Schouten Islands, all West Irian (USNM); reef at Cape Moem, nr. Wewak Territory of New Guinea (MCZ). BISMARCK ARCHIPELAGO: Feni Ids., E of New Ireland (USNM). SOLOMON ISLANDS: Nissan Id.; Green Islands (SMF); Choiseul Bay, Choiseul Id. (ANSP); Stirling Isle, Treasury Ids.; Munda, New Georgia; Pavuvu Id.; Russell Group; Lunga, Guadalcanal (all USNM); Santa Ana Id., S. of San Cristobal (ANSP).

Tectarius rusticus (Philippi, 1846)

(Pl. 388, figs. 8, 9; pls. 402, 403)

Range—Northern Western Australia.

Remarks—This species is restricted to northern Western Australia according to available locality data. It appears to be most closely related to *T. rugosus* from which it differs in its usually less regularly sculptured, more flat-sided whorls and in its lack of external coloration. In *T. rusticus* the subsutural, midwhorl and peripheral rows of spines are quite commonly strongly expressed, while in *rugosus* all rows are subequal.

Habitat—Lives on rocks above high tide line.

Description—Shell reaching about 40 mm (about 1½ inches) in length, broadly conical in shape, average obesity about .77 (29 specimens range from .72-.83); becoming moderately thick

in structure, imperforate, and sculptured with 2-3 main rows per whorl of rather muted spines. External color yellowish white with occasional faint orange stripes; inside of aperture white and occasionally tinged with pinkish orange, often with brown lines at its edge and revolving within; apertural tooth often stained with brown. Base flattened, sculptured spirally with nodulose cords, the strongest of which occurs just below periphery of body whorl. Whorls 6-8, rather flat sided. Length of spire greater than half the length



Plate 402. *Tectarius rusticus* (Philippi, 1846).

Figs. 1,2. *Litorina papillosa rustica* Philippi, knobby and smooth forms, respectively.

Fig. 2 (lectotype figure) probably is representation of Philippi's concept of *L. p. subnervis*, the smooth form; both from Point Swan, northern Western Australia; from *Abbildungen und Beschreibungen Conchylien*, vol. 2, *Litorina*, pl. 2, figs. 3,4.

of shell or the two may be about subequal. Spire convex, produced at an angle of about 68° . Aperture rounded to squarish; outer lip thickly produced, internal plicae only moderately produced and not reaching edge of aperture; outer lip tapering to thin crenulate edge; inner lip forming a tooth-like bulge anteriorly near junction with outer lip; tooth often stained with brown. Suture usually obscured by anteriormost row of spines of preceding whorl. Spiral spinose sculpture subdued, usually three rows are outstanding: the anteriormost, posteriormost and central rows of each whorl, the rest being limited to undulating, slightly bumpy cords; from 12-14 spines per row on body whorl; spines sometimes coalesce into oblique axial bars. Fine sculpture composed of microscopic wavy spiral cords and finer threads. Operculum moderate in size, circular, light-brown with a dark-brown center, paucispiral, nucleus about central. Periostracum not evident. Nuclear whorls partly decollate in all specimens examined; remaining portions smooth, white; early postnuclear whorls rapidly becoming spirally striate. Radula littorinoid, 2-1-1-1-2, similar in appearance to that of *T. rugosus*. Preserved specimens not available for observations on anatomy; radula obtained from dried specimen. Nothing reported concerning reproduction and development.

Measurements (mm) (all Western Australia)—

length	width	no. whorls	locality
35.5	29.0	5+	Yampi Sound, W.A.
34.5	27.5	6+	Cliff Id., King Sound
32.4	23.3	8+	Buccaneer Archipelago
25.8	20.6	7+	Buccaneer Archipelago
23.2	18.8	5+	Cliff Id., King Sound
22.1	17.1	6+	Buccaneer Archipelago
21.9	16.2	7+	Buccaneer Archipelago
21.1	15.3	7+	Cliff Id., King Sound
16.3	12.7	6+	Buccaneer Archipelago
15.8	12.2	6+	Buccaneer Archipelago

Synonymy—

- 1846 *Littorina papillosa rustica* Philippi, *Abbildungen und Beschreibungen Conchylien*, vol. 2, *Littorina*, p. 140, pl. 2, fig. 3 [and 4 Lectotype Figure] (Point Swan [Cape Leveque, Dampier Land, northern Western Australia]; type-specimen may be in Berlin Museum).
- 1846 *Littorina papillosa subinermis* Philippi, *ibid.*, p. 141, pl. 2, fig. 4.
- 1857 *Littorina bullata* in Reeve, *Conchologia Iconica*, vol. 10, *Littorina*, pl. 1, fig. 1c; not *Trochus bullatus* Martyn [non-binomial] which is *Tectarius grandinatus* Gmelin.
- 1971 *Tectarius pagodus* Linnaeus, Wilson and Gillett, *Australian Shells*, p. 30, pl. 11, fig. 9.

Records—WESTERN AUSTRALIA: Troughton Islands, N. of Admiralty Gulf, S.E. Wood Island, E. of Cockatoo Island; Yampi Sound; Koolan Island (all WAM); Kellan Island, Buccaneer Archipelago (AMS; USNM; MCZ); Cliff Island (USNM) all vicinity of King Sound.

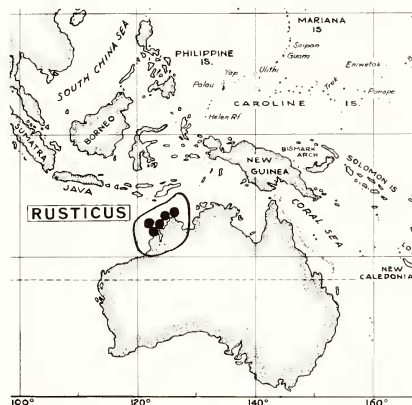


Plate 403. Geographic distribution of *Tectarius rusticus* (Philippi) in northern Western Australia.

Tectarius songoense (Martin, 1931)

(Pl. 404, figs. 3,4)

Range—Eocene of Java, Nanggoelan-beds, Kali Songo.

Remarks—It is not too difficult to determine from Martin's illustration just why he assigned this species to "*Tectarium*". There is a weakly nodulose sculpture, perhaps better described as beaded, and there appears to be a columellar tooth, a structure characteristic of Tectariinae. The general shape and appearance are, however, more suggestive of Trochidae. The species is tentatively here placed in the subfamily Tectariinae for want of positive proof to the contrary.

Synonymy—

- 1931 *Tectarium* (*Echinella*) *songoense* K. Martin, *Wetenschapelijke Mededeelingen Dienst Mijnbouw*, no. 18, p. 41, pl. 6, fig. 5, 5a, (Upper Eocene, Nanggoelanbeds, Java); unique holotype probably in Geological Museum, Leiden; length 8 mm.

Subgenus Subditotectarius Ladd, 1966

Type: *Tectarius rehderi* Ladd, 1966

Small, stout; spire conical, base convex; with beaded spiral ribs and slightly oblique axial lines; aperture strongly plicate within. Sculpture subdued, consisting of small beads formed by convergence of axial growth lines and spiral threads.

Synonymy—

1966 *Subditotectarius* Ladd, Geological Survey Professional Paper 531, p. 59; type-species by original designation: *Tectarius rehderi* Ladd.

Tectarius (Subditotectarius) rehderi Ladd, 1966

(Pl. 404, figs. 5-7)

Range—Lower Miocene, Marshall Islands.

Remarks—The fossil *Subditotectarius rehderi* is characterized by its subdued beaded sculpture as compared with *Tectarius s.s.* with its larger nodules and spines. Otherwise the species is quite similar to other *Tectarius* in outline and sculpture, and in the presence of a columellar tooth and plications within the aperture. Although apparently clearly a tectariine *S. rehderi* is not believed to be closely related to any living species.

Synonymy—

1966 *Tectarius (Subditotectarius) rehderi* Ladd, Geological Survey Professional Paper 531, p. 59, pl. 11, figs. 11-13 (drill hole 2A, Bikini Atoll, 1,051-1,057 feet; early miocene); holotype USNM 648342, 2.8×2.4mm.

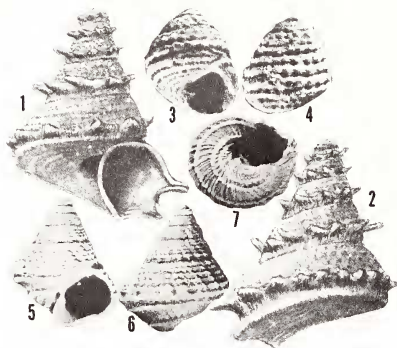


Plate 404. Fossils of Tectariinae and Echinininae.

Figs. 1, 2. *Echininus adelaidensis* (Cotton, 1947) holotype, 16 × 12 mm.

Figs. 3, 4. *Tectarius songoense* Martin, 1931; holotype, 8 mm length.

Figs. 5-7. *Tectarius rehderi* Ladd, 1966, holotype, 2.8 × 2.4 mm.

Subfamily Echinininae, new subfamily

Genus Echininus Clench and Abbott, 1942

Type: *Echininus cumingi* (Philippi, 1846)

The genus *Echininus sensu lato* includes the nominate subgenus, *Echininus*, typified by the umbilicate and spinose *E. cumingi* and also *E. cumingi spinulosus*, both of the western Pacific, and the subgenus *Tectininus* Clench and Abbott, 1942, having the non-umbilicate and less spinose monotype, *E. (T.) nodulosus* (Pfeiffer), a species which inhabits the Caribbean area. Members of both subgenera have what may be called multispiral (polygyrous spiral type) opercula and possess moderately spinose shells. In *Echininus sensu stricto* the central radula tooth is moderately reduced in width, while in *Tectininus* it is dramatically reduced and narrowed. Abbott (1954) discussed the phylogenetic position of *Echininus* and concluded that it belongs in Littorinidae although it possesses many specialized characters such as the multispiral operculum, an umbilicus and a narrow central radula tooth. As there are no representatives of *Tectininus* in the Indo-Pacific, only *Echininus s.s.* will be considered here.

Synonymy—

1854 *Echinella* 'Swainson' H. and A. Adams, The Genera of Recent Mollusca, vol. 1, p. 316; three species mentioned: *coronaria* Lamarck [= *Tectarius grandinatus* Gmelin]; *granulata* Swainson [unrecognizable]; and the exemplary species, *cumingii* Philippi; 1895, Pilsbry, Catalogue of the Marine Mollusks of Japan, p. 175; 1901, Pilsbry, Proceedings of the Academy of Natural Sciences of Philadelphia, p. 198; 1903, Kesteven, Proceedings of the Linnean Society of New South Wales, for 1902, part 4, p. 632, in part; not *Echinella* Swainson, 1840 [= *Tectarius s.s.*].

1942 *Echininus* Clench and Abbott, Johnsonia, vol. 1, no. 4, p. 3; new name for *Nina* Gray, 1850, Figures of Molluscan Animals, London, vol. 4, p. 78; Type species by monotypy *Trochus cumingii* Philippi; not *Nina* Horsfield, 1829, nor Gray, 1855.

Subgenus Echininus s.s.

Pyramidal, umbilicate littorinids with a strongly spinose shell. In males the penis has a deep but open sperm duct, and basal penial glands are present. Operculum multispiral. Radula littorinoid, the central tooth moderately narrow.

Echininus cumingi cumingi (Philippi, 1846)

(Pl. 388, figs. 12, 13)

Range—From the Philippines along the western Pacific arc to New Hebrides and the Cook Islands.

Remarks—At first examination one finds it surprising that "*Cuming's Echininus*" is included in the Littorinidae. This species has many of the attributes of certain other families, perhaps resembling most some members of the family Trochidae with its conical shape, multispiral operculum and well-defined umbilicus. Animal characters, especially the radula, and gross reproductive features leave no doubt, however, that *E. cumingi* is a littorinid. Its closest relative is the smaller and less spinose, but otherwise very similar appearing subspecies, *E. cumingi spinulosus* (Philippi). The next most closely related and only other species in the subfamily, the Western Atlantic *E. (Tectininus) nodulosus* (Pfeiffer) differs in never being umbilicate and in having a considerably more reduced radula. The open condition of the spines occurs occasionally in *E. nodulosus* and their arrangement or alignment is similar. Both have multispiral opercula. Penial anatomy differs, however, *E. cumingi* having a cluster of basal penial glands, whereas *E. nodulosus* displays a basal swelling and a single gland located one half to two thirds the distance to the tip (see Abbott, 1954, fig. 55, p.q).

Habitat—Lives in pockets of weathered, raised limestone reef, 3-7 meters above high tide line (personal observations in Davao, Philippines and Moluccas Islands, 1970).

Description—Shell reaching 20.4 mm (about 3/4 inch) in length, broadly conical in shape, with



Plate 405. *Echininus cumingi cumingi* (Philippi, 1846). *Trochus cumingii* Philippi, lectotype figure of specimen in BM(NH), from Reeve, 1857, Conchologia Iconica, vol. 10, Littorina, pl. 2, fig. 8.

projecting spines, average obesity about .88 (33 specimens range from .77 to 1.03) only moderately thick in structure, umbilicate; suture impressed, whorls slightly rounded; sculptured with three rows of short, projecting, often unclosed spines. External shell color grayish tan, the spines often being reddish brown; a thin grayish brown periostrical coating apparent; aperture a diffuse yellowish to reddish brown, occasionally with three reddish brown color bands reflecting the position of the external spines. Base distinctly flattened, spirally sculptured with nodulose cords of which about the third below the periphery is the strongest. Umbilicus very deep but narrow in mature specimens; bordered medially by a rim of the columellar callus and distally by a basal fold. Whorls 6-8, only slightly rounded. Length of spire greater than half the length of the shell. Spire convex, produced at an angle of from about 66-76°. Aperture rounded, outer lip only moderately thickened, smooth within, the edge often undulating in the vicinity of the rows of spines; inner lip curved and shining, edentulous. Suture usually somewhat obscured by anteriormost row of spines of preceding whorl. Primary sculptural feature is the three spiral rows of spines. Posteriormost row of spines consisting of low, rounded protuberances; anteriormost row small, unclosed, moderately projecting, narrow-hoodlike and closely spaced; middle row of spines largest, most projecting, also incompletely closed. Rows of spines not aligned axially; spine count as follows: anterior row, 18-25; middle row, 14-17; posterior 15-16 (approximate range). Secondary spiral sculpture between rows of spines consists of from 4-6 slightly raised cords; overall microscopical spiral sculpture of fine, closely spaced threads. Axial sculpture consists of fine irregular often overlapping lines of growth. Operculum moderate in size, multispiral (polygyrous spiral type) having about 5-7 volutions, chitinous, dark-brown (pl. 389). Nuclear whorls smooth, light brown, shining, about 1.5 volutions; postnuclear whorls rapidly becoming striately sculptured and then spinose. Radula littorinoid, 2-1-1-1-2, central tooth very narrow, rather simple; lateral tooth only moderately narrow and with a well developed littorinoid notch.

Animal littorinoid; penis large and well-developed, with a bulbous swelling at its base; distal extremity simple; with as many as 12 penial glands clumped mostly on posterior surface near junction of bulbous base and extremity; sperm

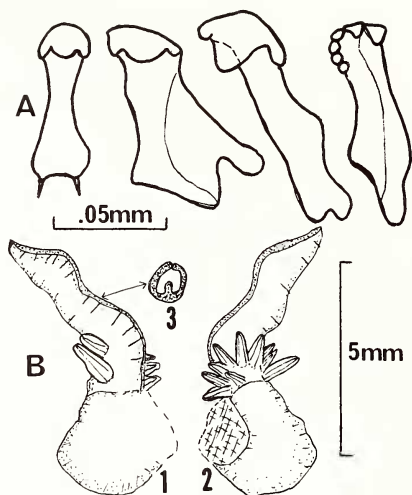


Plate 406. *Echinus cumingi* (Philippi).

Fig. A. Radula; note "spurs" on central tooth, and generally narrow dentition.

Fig. B. Penis. 1, anterior, 2, posterior, 3, cross-section of seminal groove; note cluster of glands near bulbous base (both from Davao Gulf, Mindanao, Philippines).

groove deeply folded, with an apparent internal fold best seen distally. Details of reproduction and life history unknown.

Measurements (mm)—

length	width	no. whorls	locality
20.4	17.3	7	Cook Islands
19.5	17.6	8	Philippines
18.5	14.9	7+	Stirling Isle, Treasury Ids., Solomons
17.5	14.3	7+	Stirling Isle, Treasury Ids., Solomons
17.0	14.9	7	Cook Islands
16.7	15.3	7+	Cook Islands
16.3	14.8	7+	Stirling Isle, Treasury Ids. Solomon Ids.
15.9	12.3	7+	Stirling Isle, Treasury Ids. Solomon Ids.
15.1	13.0	7+	Tana, New Hebrides
14.6	13.7	6+	Stirling Isle, Treasury Ids. Solomon Ids.
13.2	11.9	7+	Stirling Isle, Treasury Ids. Solomon Ids.
10.6	10.9	8	Philippines

Synonymy—

1846 *Trochus cumingi* Philippi, Proceedings of the Zoological Society of London, for 1845, p. 138 (Guimaras Id. [south of Panay Id.] Philippines; as *Litorina*, 1847. *Abbildungen und Beschreibungen Conchylien*, vol. 3,

Litorina, p. 53, pl. 6, fig. 22; lectotype in BM (NH), figured by Reeve, 1857, *Conchologia Iconica*, vol. 10 *Littorina*, pl. 2, fig. 8.

- 1879 *Trochus echinulatus* 'Kiener' in P. Fischer, *Spécies Général et Iconographie des Coquilles Vivantes*, pl. 43, figs. 2 [name and figure only]; *ibid.*, p. 459, places name in synonymy of *Tectarius cumingi* (sic); not *Trochus echinulatus* A. Alth, 1850.

Records—PHILIPPINES: Samal Id., Davao Bay, Mindanao (USNM, MCZ). INDONESIA: Karakelong Id., Taland Ids. (MCZ); N. shore Warbal Id., W of Nuhu Rowa, Kai Ids.; W. side Mitak Id., Jandena Strait, Tanimbar, both Moluccas (USNM, WAM). NEW GUINEA: Misool; Fakfak (both RNHL); Louisiade Ids. (RNHL, NMW, ANSP). SOLOMONS: Stirling Isle, Treasury Ids., (USNM); Santa Ana (ANSP). NEW HEBRIDES: S end Black Beach, Tana (USNM). COOK ISLANDS: Manke, Hervey Ids.; Rarotonga (both ANSP); Mangaia (USNM).

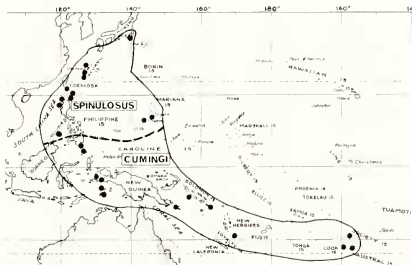


Plate 407. Geographic distribution of *Echininus cumingi* (Philippi) in the East Indies and Pacific Ocean, and of its more northerly distributed subspecies *E. cumingi spinulosus* (Philippi).

Echininus cumingi spinulosus (Philippi, 1847)

(Pl. 388, figs. 14, 15; pls. 407, 408)

Range—From southern Japan through the Ryukyu Islands, the northern and western Philippines and eastward to the Mariana Islands.

Remarks—*Echininus spinulosus* is very close in its relationship to *E. cumingi*, the differences between the two being more of degree than of kind. The two are apparently geographically isolated, or at least they occupy separate ranges and so the phenotypic differences may be ecologically influenced as well as having a genetic basis. Whatever the basis for the differences between them, it seems appropriate to consider them as subspecies. *Echininus spinulosus* never reaches as large a size or achieves the squatly conical shape of *E. cumingi*, and although the sculpture of the two is basically very similar, *cumingi* is always more distinctly spinose. Both are usually umbilicate although *spinulosus* is often narrowly

so and young specimens may lack this feature entirely, as did Philippi's type-specimen.

It is interesting to note that *E. luchuana* was described by Pilsbry (1901) as a subspecies of *cumingi*, which has caused some confusion. Some malacologists have continued to use the combination *E. cumingi luchuana* or simply *E. cumingi* when referring to the entity *E. spinulosus* (Kira, 1959, 1962; Habe, 1951). Philippi's figures (1847) clearly show the species concepts he intended: *E. spinulosus* (fig. 24), the smaller less pronouncedly spinose species (which includes *luchuana* as a synonym) and *E. cumingi* (fig. 22), the larger and more outstandingly spinose and more squatly conical species.

Habitat—On rocks above the high tide line.

Description—Shell reaching 16.8 mm (about $\frac{3}{8}$ inch in length, turbanate in shape, with short spines; average obesity about .84 (32 specimens range from .74–1.08) moderately thick in structure, mature specimens usually umbilicate; suture evident although often obscure; whorls moderately rounded; sculptured with three major rows of short spines per whorl. External shell color grayish to tannish orange, the short spines usually appearing whitish; apertural coloration

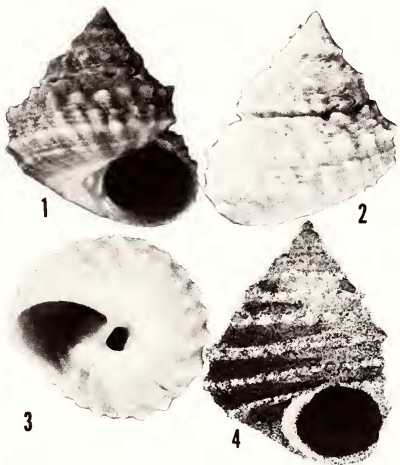


Plate 408. *Echininus cumingi spinulosus* (Philippi, 1847)

Figs. 1–3. *Echinella cumingi luchuana* Pilsbry, lectotype, ANSP 70962, 16 × 14 mm.

Fig. 4. *Litorina spinulosa* Philippi, lectotype figure, from *Abbildungen und Beschreibungen Conchylien*, vol. 3, *Litorina*, pl. 6, fig. 24.

tannish to brownish orange, occasionally with 3-4 darker brown color bands revolving within. Base moderately flattened, sculptured with nodulose cords of which about the third below the periphery is the strongest. Umbilicus usually rather narrow and occasionally absent, bordered medially by a rim of the columella callus and distally by a poorly to well defined basal fold. Whorls 6-8, only moderately well rounded. Length of spire greater than half the length of the shell. Spire convex, produced at an angle of from about 63-68°. Aperture rounded-oval, outer lip thin to only moderately thickened, smooth within, and often slightly undulating in vicinity of external spine rows; inner lip curved and shining, edentulous. Suture fairly evident to somewhat obscured by anteriormost row of spines of preceding whorl. Primary sculptural feature is three spiral rows of spines located centrally, anteriorly and posteriorly on each whorl; spiral cords between main rows tending to become nodular to spinose. Rows of spines not well aligned axially; spine count as follows: anterior row about 24; middle row about 19-23; posterior row about 16-19. Secondary sculpture consisting of 4-5 rows of spiral cords which occasionally become nearly as strongly spinose as the 3 primary rows which they separate; overall microscopical spiral sculpture of fine, closely-spaced threads. Axial sculpture consists of fine irregular lines of growth. Operculum small to moderate in size, multispiral (polygyrous spiral type) having 5-6 volutions, chitinous, dark brown. Nuclear whorls smooth, tannish white, shining, about 1.5 volutions; postnuclear whorls rapidly becoming striated and nodulose. Radula littorinoid, 2-1-1-1-2; central tooth narrow and reduced; lateral tooth with a distinct littorinoid notch. Animal littorinoid; penis unbranched, a well developed sperm groove running along its medial edge; distal portion papillose; 2-3 penial glands located half-way between base and tip in preserved specimen. Nothing has been reported concerning reproduction and life history.

Measurements (mm)—

length	width	no. whorls	locality
16.8	11.7	8	Fuga Id., Philippines
15.6	12.2	7+	"Japan"
14.9	11.1	7+	Yokohama, Japan
14.2	11.8	7	Batan Id., Philippines
13.9	11.5	6+	Batan Id., Philippines
13.5	10.9	8	Batan Id., Philippines
13.0	10.4	7	Kume-shima, Ryukyu Ids.
12.6	10.4	6+	Okinawa, Ryukyu Ids.

12.0	10.0	7+	Batan Id., Philippines
11.1	9.0	7	Batan Id., Philippines
10.8	10.5	7	Batan Id., Philippines
7.3	7.9	6	Batan Id., Philippines

Synonymy—

- 1847 *Litorina spinulosa* Philippi, *Abbildungen und Beschreibungen Conchylien*, vol. 3, *Litorina*, p. 53, pl. 6, fig. 24. Lectotype Figure (Manila); type may be in Berlin Museum.
- 1895 *Echinella cumingi* Phil. in Pilsbry, *Catalogue of the Marine Mollusks of Japan*, published by Frederick Stearns, Detroit, p. 175 (Yaeyama [Okinawa]).
- 1901 *Echinella cumingi luchuana* Pilsbry, *Proceedings of the Academy of Natural Sciences of Philadelphia*, p. 198 (Loo Choo Islands [Ryukyu Islands]); *ibid.* p. 394, pl. 19, fig. 16; lectotype ANSP 70962, ca. 16 × 14 mm.

Records—JAPAN: Yokohama (USNM). RYUKYU ISLANDS: Kadena Circle (USNM); Tsukin-shima, both Okinawa (MCZ); Kume-shima (MCZ ANSP, USNM, BPBM); Karimata, Miyako-shima (MCZ, ANSP); Ora Wan (USNM). TAIWAN: Hung-tou Hsu, off Pacific Coast (ANSP, USNM). PHILIPPINES: Santa Domingo de Basco, Batan, Batan Ids. (USNM); Dalupiri Id. (MCZ); Fuga Id., both Babuyan Ids. (USNM); Camp Wallace, Province of La Union, Luzon; Puerto Princesa, Palawan (both USNM). MARIANA ISLANDS: Saipan; Piti Bay, Guam (both ANSP); Apra Bay; Asan Point, both Guam (both USNM).

Echininus adelaidensis (Cotton, 1947)

(Pl. 404, figs. 1,2)

Range—Adelaidean (Pliocene), South Australia.

Remarks—*Echininus adelaidensis* certainly is a unique appearing species which somewhat resembles certain of the Trochidae nearly as much as it does *Echininus* (cf. *Turcica* A. Adams or *Perrinia* H. and A. Adams, as shown in Wenz, 1938). The characteristics of its partly open spines and the presence of an umbilicus may be sufficient to relate it to *Echininus*, however. Cotton refers to *E. cumingi* Philippi having been collected in Caloundra, Queensland and Western Australia, but I have not seen such records in the course of the present study. It is possible that northern portions of Australia may be within the range of *E. cumingi* which reaches the southern Moluccas and New Guinea.

Synonymy—

- 1947 *Nina adelaidensis* Cotton, *Records of the South Australian Museum*, vol. 8, no. 4, p. 666, pl. 21, figs. 17, 18 (Adelaidean Pliocene, Salisbury Bore, 350 feet); holotype in Tate Museum, University of Adelaide, 16 × 12 mm.

"Littorina" incisa Yokoyama, 1927

(Pl. 358, figs. 4, 5)

Range—Pliocene of Japan.

- ★ *Remarks*—As pointed out by Habe (*in litt.*, 1971), this 5 mm. shell is a member of the Pyramidellidae. We erroneously considered it to be a *Littorina* (*Littorinopsis*) in our last number of Indo-Pacific Mollusca, vol. 2, no. 11, p. 466 [p. 05-340], pl. 358, figs. 4, 5.

Synonymy—

- 1927 *Littorina incisa* Yokoyama, Journal of the Faculty of Science, Imperial University of Tokyo, section II, Geology, Mineralogy, Geography, Seismology, vol. 2, part 4, p. 175, pl. 47, fig. 8 (Pliocene, Nagaya, Kaga, Japan); holotype in Geological Institute, Imperial University of Tokyo; 5 × 2.5 mm.
- 1970 *Littorina incisa* Yokoyama, Rosewater, Indo-Pacific Mollusca, vol. 2, no. 11, p. 466.

Littorina kozaiensis Nomura and Onisi, 1940

(Pl. 349, figs. 6, 7)

Range—Lower Miocene of Japan.

Remarks—This species was described as resembling *L. adonis* Yokoyama (see below), but as having a larger number of spiral grooves. The unique holotype (pl. 349, figs. 6, 7, a copy of the original illustration) offers little basis for comparison with Recent species.

Synonymy—

- 1940 *Littorina kozaiensis* Nomura and Onisi, Japanese Journal of Geology and Geography, vol. 17, nos. 3 and 4, p. 191, pl. 19, fig. 6 a,b. (Yōsuibori, Simizu, Kozaimura, Japan); holotype; Saitō Hō-on Kai Museum, Register No. 21762; 11 × 8 mm.

Littorina adonis Yokoyama, 1927

(Pl. 349, figs. 8, 9)

Range—Pliocene of Japan.

Remarks—Placed provisionally here in the subgenus *Littoraria*, this species resembles *L. undulata*, although the strong spiral sculpture is also reminiscent of *Littorinopsis*, i.e. *L. scabra*, etc. Unfortunately the outer lip and a portion of the body whorl of the type (pl. 349, figs. 8, 9) are missing and it is difficult to be sure of their exact shape.

Synonymy—

- 1927 *Littorina adonis* Yokoyama, Journal of the Faculty of Science Imperial University of Tokyo, section 2, vol. 1, part 10, p. 451, pl. 51, fig. 8. (Upper Musashino, Koyasu southern Musashi, Japan); (unique holotype in collection of Geological Institute Imperial University of Tokyo; 6 × 4 mm.).

Littorina lucida Yokoyama, 1927

(Pl. 349, figs. 4, 5)

Range—Pliocene of Japan.

Remarks—This species is from the same deposit as *L. adonis* but lacks the deeply incised spiral sculpture. The type of *lucida*, although of approximately the same size as *adonis* is more slender.

We overlooked the fact that Habe, 1942 (Venus, vol. 12, p. 37) and Abbott, 1958 (Proc. Acad. Nat. Sci. Phila., vol. 110, p. 270) had pointed out that *L. lucida* was a synonym of *Assiminea japonica* von Martens, 1877. ★

Synonymy—

- 1927 *Littorina lucida* Yokoyama, Journal of the Faculty of Science Imperial University of Tokyo, section 2, vol. 1, part 10, p. 451, pl. 51, fig. 9 (Upper Musashino, Koyasu southern Musashi, Japan); (unique holotype in collection of Geological Institute Imperial University of Tokyo; 5 × 3 mm.).

[*These occasional blank areas occur between genera and subgenera to permit the insertion of new material and future sections in their proper systematic sequence.*]